an anther on the staminodial side. The stamens present ranged in number from one to five and the styles from two to four. In no case were the perianth segments modified in any way.

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CYTOPHYLETIC ANALYSIS OF CERTAIN ANNUAL AND BIENNIAL CRASSULACEAE

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An attempt is here made to analyze from a cytophyletic viewpoint the relationship existent among several annual and biennial Crassulaceae, a family predominantly perennial. Such an analysis necessarily passes from fact to hypothesis, but the analysis should be made. Observations isolated have restricted meaning; from them integrated, hypotheses may be formulated and, with the accumulation of evidence, may be re-examined and tested.

The systematic history of certain of the species considered is a record of many taxonomic maneuvers. That history is reviewed. Each different taxonomic concept of a plant should be indicative of that plant's affinities. The plants treated here will doubtless be subjected to other changes in nomenclature. And that is as it should be. "There is no finality in taxonomy" (L. H. Bailey).

Sedum pusillum Michx.

Michaux (20, 1803) described as *Sedum pusillum,* a small, octandrous, white-flowered plant from Flat-rock, North Carolina. Pursh (22, 1814), apparently confusing Michaux's species with the plant later designated *S. Nevii* Gray, reported *S. pusillum* to be perennial and to occur in Virginia "on the east banks of the Shanadoah River." Nuttall (21, pp. 110, 293, 1818) included *S. pusillum* as a synonym of his *Tillaea ? cymosa* and (21, p. 293) made both *Tillaea ? cymosa* and *Sedum pusillum* synonymous with *Diamorpha pusilla.* Gray (17, 1876) first recognized that Nuttall and subsequent writers had confounded two species and that *Sedum pusillum* and *Diamorpha pusilla* are distinct. Gray, in 1875, found them both in great abundance on Stone Mountain in Georgia; Canby had collected the two there in 1869 but had not differentiated between them. Rose (24, 1905) established for Michaux's species the monotypic genus *Tetrorum;* Berger (6, 1930) and Fröderström (16, 1935) again referred the plant to *Sedum.* The species is known only from North Carolina and Georgia. As treated by Fröderström, the species has narrowly spurred leaves, 4- to 5-parted flowers with white or purple petals broad at the base, immature carpels suberect and broad-styled,

mature carpels horizontally spreading, tillaeoid, and very short-styled, and ovoid seed.

Plants of *Sedum pusillum* were grown at Charlottesville, Virginia, and at Ithaca, New York, from seed collected on Stone Mountain by Dr. Edgar T. Wherry. (The identity of each species investigated during the present study was checked by Dr. R. T. Clausen of the Bailey Hortorium.) The chromosomes were studied in smears of roots, leaves and anthers. The somatic smear method has been discussed by the present author (4, 1938). The $2n$-number of the species is 8 (pl. 17, fig. 1), and the n-number is 4 (pl. 17, fig. 2, second metaphase; fig. 3, second anaphase). Each chromosome has a median or submedian constriction. The four pairs of chromosomes are distinguishable at somatic metaphase (pl. 17, fig. 1).

Sedum stellatum L.

Sedum stellatum, described by Linnaeus, is an annual of the Mediterranean region. Fröderström (15, 1932) characterized the species as having shortly petiolate leaves with obovate-orbiculate blades, 4- to 5-parted, purplish-red flowers with petals "free to the base" and with "mature carpels stellate, connate 1.5–2 mm., with a long and narrow gibbosity," and ovoid seed. Two lines of *S. stellatum,* B325 and C142, in cultivation at Cornell University have been examined cytologically. The species has a $2n$-number of 10 (pl. 17, fig. 4) and an n-number of 5 (pl. 17, fig.5, first metaphase; fig. 6, first anaphase; fig. 7, second anaphase). The five pairs of chromosomes are distinguishable at somatic metaphase (pl. 17, fig. 4).

Sedum Nuttallianum Raf.

Rafinesque, in 1832, established *Sedum Nuttallianum* for an annual plant distributed from Missouri and Arkansas to Texas. The species, as treated by Fröderström (16, 1935), has broadly spurred, oblong leaves, 5-parted, yellow, sessile flowers with "petals united with their broad bases" and with "carpels united 1 mm., gibbous and stellate," and ovoid, mammillate seed. Plants of *S. Nuttallianum* were collected near Georgetown, Texas, by Dr. Gordon B. Wolcott. The writer found those plants to have a $2n$-number of 20 (pl. 17, fig. 8), an n-number of 10 (pl. 17, fig. 9, first metaphase).

Sedum annuum L.

Linnaeus described *Sedum annuum.* Berger (6, 1930) placed the species systematically adjacent to *S. Nuttallianum. Sedum annuum* is annual or, sometimes, by means of small, sterile shoots, perennial (Fröderström, 15, 1932); at Ithaca, New York, the species is seemingly perennial. It is distributed from "Caucasus through Asia Minor, Russia and Europe to Greenland." The plant has bluntly spurred, "linear-oblong to obovate" leaves,

5-parted, yellow to greenish-yellow, sessile flowers, "carpels stellate in fruit, connate 0.7–1 mm.," and ovoid seed. Böcher (7, 8, 1938) reported an *n*-number of 11 for *S. annuum* as represented in Greenland. Three lines of the species have been investigated during the present study: V122 at The Blandy Experimental Farm, C105 and W221 at Cornell University. A somatic number of 22 chromosomes (pl. 17, fig. 10) and a gametic number of 11 (pl. 17, fig. 11, first metaphase; fig. 12, second metaphase) were determined.

Diamorpha Nutt.

Nuttall (21, 1818) founded *Diamorpha,* the name meaning "deformed or contrary formed":—"in the structure of the capsule it entirely differs from every other plant in the Natural Order Sempervivae." (The Crassulaceae were established in their true limits in 1789 by A. L. de Jussieu under the name Sempervivae, a name assigned by Linnaeus and Bernard de Jussieu to a more comprehensive group including the present Crassulaceae and several other families; the name Crassulaceae was given the family in 1805 by A. P. De Candolle.) De Candolle (11, 1828) placed *Diamorpha,* with *Penthorum* L., in the tribe Crassulaceae Anomalae. Torrey and Gray (28, 1840) made the tribe Diamorpheae for these two genera and gave the following description of *D. pusilla:* "Carpels 4, united below the middle, tapering into short styles, when old divergent above, not dehiscent by either suture, but by the vertical separation of the dorsal portion (nearly half) of each carpel in a valvular manner . . . its remarkable dehiscence so analogous to that of *Penthorum.*"

In distinguishing *D. pusilla* from *Sedum pusillum,* Gray (17, 1876) wrote: "The *Diamorpha,* of barely half the size, and with proportionally wider leaves, has a dull purplish hue, extending more or less to the flowers; the sepals are distinct nearly to the base and narrower; the petals oval and obtuse; the ovaries and pods tapering from a broader base into a subulate style; the seeds round-oval; and the cruciform union of the pods at base and their peculiar dorsal valvular dehiscence, peculiar to the genus . . ."

Britton (10, 1905) made the combination *Diamorpha cymosa* (Nutt.), thus rendering *D. pusilla* synonymous; he designated as *D. Smallii* a plant of localized distribution in North Carolina. Fröderström (16, 1935) made the combinations *Sedum cymosum* (Nutt.) Fröd. var. *Smallii* (Britt.). The generic status of *Diamorpha* is recognized here. The genus occurs from North Carolina and Tennessee to Georgia and Alabama.

Cytological study has been made of *Diamorpha cymosa* (Nutt.) Britt., from Stone Mountain in Georgia (seed collected by Dr. Edgar T. Wherry), from Eight-Acre Rock, Bibb County, Alabama (seed and plants collected by Dr. A. V. Beatty), and from

Rocky Face Mountain, west of Statesville, North Carolina (plants collected by Dr. C. E. Raynal and sent to the writer by Dr. W. C. Coker). The species has a $2n$-number of 18 (pl. 17, fig. 13) and an n-number of 9 (pl. 17, fig. 14, first metaphase; fig. 15, second metaphase).

Sedella Britt. and Rose

The genus *Sedella,* originally characterized by having flowers with yellow petals united at the base, ten stamens, one-seeded, oblong carpels, and erect seed, was established by Britton and Rose (9, 1903) for two Californian annuals first described as species of *Sedum: Sedum pumilum* Bentham (5, 1849) and *Sedum Congdoni* Eastwood (12, 1898). Jepson (18, 1925) made the combination *Sedella pumila* (Benth.) Britt. and Rose var. *Congdoni* (Eastw.). Berger (6, 1930) restored these plants to *Sedum* as two species of section *Sedella.* Fröderström (16, 1935) made the combination *Sedum pumilum* Benth. var. *Congdoni* (Eastw.); he considered this to be the only species of the group *Sedella.* Sharsmith (26, 1936) resurrected the genus *Sedella* and published a third species, a Californian annual, *S. pentandra.* That writer has now described a second pentandrous species (27).

At the request of Mrs. Sharsmith, Dr. Herbert L. Mason, of the University of California Herbarium, sent the writer, on January 18, 1938, seeds from the following herbarium specimens: *Sedella pentandra,* Sulphur Creek, San Antonio Valley, Mount Hamilton Range, Santa Clara County, California, June 8, 1935, *H. K. Sharsmith 3271; Sedella pumila,* Napa, Napa County, California, May 31, 1935, *H. L. Mason; Sedella Congdoni,* Porterville, Tulare County, California, May 13, 1935, *W. B. Richardson.* By the end of May, 1938, plants from those seeds were in flower in the greenhouses of Cornell University. A $2n$-number of 18 for each of the species—*S. pentandra* (pl. 17, fig. 16), *S. Congdoni* (pl. 17, fig. 17), and *S. pumila* (pl. 17, fig. 18)—and an n-number of 9 for two of them—*S. Congdoni* (pl. 17, fig. 19, first metaphase) and *S. pumila* (pl. 17, fig. 20, second metaphase)—were determined. Each chromosome was observed at somatic metaphase to have a median to submedian constriction. Chromosome number and morphology, therefore, seem not to be differential characters for these species.

Discussion

The plants treated in this paper are representatives of subfamily Sedoideae and, with the exception of the *Sedella* species, have at some time been placed in close taxonomic association. *Sedella* and *Diamorpha* may be expressions of parallel tendencies in the evolution of the Crassulaceae. Both genera are non-perennial. Both afford evidence of an intimate relationship with members of subfamily Crassuloideae: some species of *Sedella* are pentandrous, and the chief distinguishing character of the Crassuloideae is the presence of only a single whorl of stamens (Berger,

6, 1930); the carpels in *Diamorpha* (as in *Sedum pusillum*) are tillaeoid (Fröderström, 16, 1935), and *Tillaea* is an annual complex of the Crassuloideae. Moreover, *Sedella* and *Diamorpha* have a gametic number of 9, and this number is rare among those determined for the family; the other cases known for the family proper are a species of *Rosularia* Stapf and one of *Cotyledon* L., these being the only chromosomally studied members of the two genera. In the "Index Kewensis," *Rosularia* is reduced to *Umbilicus* DC., which in turn is largely included in *Cotyledon;* Berger (6, 1930) referred the first of these genera to the Sedoideae, the other two to the Cotyledonoideae. Then there is *Penthorum sedoides* L. Rocén (23, 1928) reported the *n*-number of Asiatic and American plants of this species to be 8; the present writer, working with the species in Virginia, found a 2*n*-number of 18, *n*-number of 9. Since the gametic number of 9, unusual for the family, occurs in *Penthorum* and *Diamorpha,* it is perhaps phyletically significant that, as mentioned above, De Candolle (11, 1828) and Torrey and Gray (28, 1840) placed these genera together as being peculiar. By other workers, *Penthorum,* variously conceived to include from one to three species, has been referred to the Crassulaceae (Schönland, 25, 1891), to the Saxifragaceae (Baillon, 2, 1872; Engler, 13, 1930), and to a family of its own, the Penthoraceae (van Tieghem, 29, 1899). Embryological studies indicate that the genus belongs in the Saxifragaceae but shows kinship with the Crassulaceae (Mauritzon, 19, 1933). Evidence given in the present instance would seem to favor the placement of the genus in the latter family. But the entire discussion well illustrates that affinities among plants are both linear and interlinear, evolutionary trends being sometimes confluent, and that taxonomic categories are discrete with respect to certain characters, continuous with respect to others.

Sedum pusillum has a somatic chromosome number of 8, a gametic number of 4. These numbers are the lowest known for the Crassulaceae and are to be contrasted with a 2*n*-number of *ca.* 500, in a species of *Kalanchöe* L. (Baldwin, 4, 1938), as the highest. *S. pusillum* has tillaeoid carpels (Fröderström, 16, 1935),

Explanation of the Figures, Plate 17.

Plate 17. Chromosomes of Certain Crassulaceae. Figs. 1–3, *Sedum pusillum,* 2n = 8, n = 4: fig. 1, somatic metaphase; fig. 2, second metaphase; fig. 3, second anaphase. Figs. 4–7, *Sedum stellatum,* 2n = 10, n = 5: fig. 4, somatic metaphase; fig. 5, first metaphase; fig. 6, first anaphase; fig. 7, second anaphase. Figs. 8–9, *Sedum Nuttallianum,* 2n = 20, n = 10: fig. 8, somatic metaphase; fig. 9, first metaphase. Figs. 10–12, *Sedum annuum,* 2n = 22, n = 11: fig. 10, somatic metaphase; fig. 11, first metaphase; fig. 12, second metaphase. Figs. 13–15, *Diamorpha cymosa,* 2n = 18, n = 9: fig. 13, somatic metaphase; fig. 14, first metaphase; fig. 15, second metaphase. Figs. 16–20, *Sedella,* 2n = 18, n = 9: fig. 16, *S. pentandra,* somatic metaphase; fig. 17, *S. Congdoni,* somatic metaphase; fig. 18, *S. pumila,* somatic metaphase; fig. 19, *S. Congdoni,* first metaphase; fig. 20, *S. pumila,* second metaphase. Magnification: fig. 11 drawn ×4900, the other figures, ×3700, and reduced about three-fifths in reproduction.

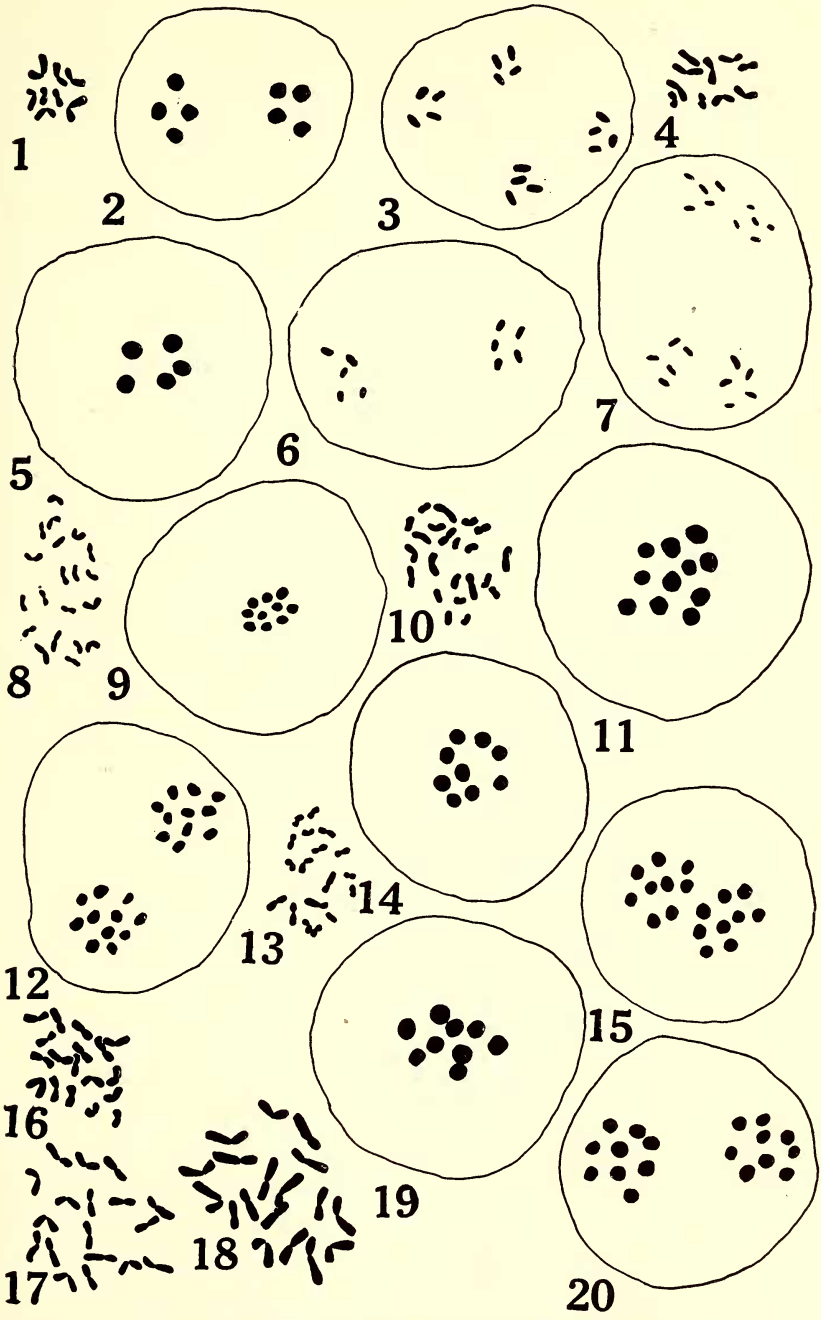

PLATE 17. CHROMOSOMES OF CERTAIN CRASSULACEAE.

and the *Tillaea*-complex is considered to be primitive (Fröderström, 14, 1930; Berger, 6, 1930). The members of that complex cytologically investigated have somatic numbers of 16 (Baldwin, 3, 1936). It is logical, therefore, to consider that 4 is the initial or one of the initial chromosome numbers of the family.

Sedum stellatum has an *n*-number of 5. This species is usually associated with the *Sedum hispanicum*-complex of the genus, and some representatives of that complex have *n*-numbers of 15 and 20 (Baldwin, ms.). Fröderström (16, 1935) suggested that *S. stellatum* be compared with his group consisting of *S. pusillum*, *S. Nuttallianum*, and *S. cymosum* (*Diamorpha cymosa*): *S. Nuttallianum* has an *n*-number of 10. Thus, there exists in *Sedum* a 5-chromosome system, and this, like the 4-chromosome system, has at the lower extreme of its polyploid series non-perennial species. It is likely that one of these systems deviated from the other. So, also, it is reasonable that the *Diamorpha* and *Sedella* aggregates, with an *n*-number of 9, are the amphidiploid results of fusions between representatives of the 4- and 5-chromosome tendencies. This possibility is an additional basis for the treatment of *Diamorpha* and *Sedella* as entities of generic rank. Further, we may consider that the farther, temporally and physically, the primitive developmental streams got from their locus of bifurcation, the more dissimilar, in general, they became. And similarly: the more different was the result of each successive intermingling of those streams. If the products of such unions then underwent a doubling of chromosomes—became amphidiploid, the immediate origin of "categories higher than a species" might be expected (Anderson 1, 1937). It is interesting, therefore, that: *Sedella* and *Diamorpha* are often regarded as genera of questionable standing; *Rosularia* is placed at the periphery of the Sedoideae; *Cotyledon* is the type of another subfamily; *Penthorum* is a genus of uncertain familial affinities, and all these groups, apparently constituting an evolutionary series of greater and greater morphologic diversity, have an *n*-number rare among those known for the Crassulaceae. Incidentally, the series supports the view that in this family life-duration was primitively non-perennial.

Summary

Cytotaxonomic data show that certain annual and biennial Crassulaceae may be referred, theoretically, to primitive 4- and 5-chromosome systems and to an amphidiploid system originating from these: *Sedum pusillum* has 8 somatic, 4 gametic chromosomes; *S. stellatum*, 10 and 5 respectively; *S. Nuttallianum*, 20 and 10; *Diamorpha cymosa*, 18 and 9; *Sedella pentandra*, *S. Congdoni*, and *S. pumila*, 18 and 9. *Sedum annuum*, behaving sometimes as a perennial, has 22 somatic, 11 gametic chromosomes; this species has, on occasion, been placed systematically close to *S. Nut-*

tallianum. The $2n$-number, 8, in *S. pusillum* is the lowest known for the family and contrasts with *ca.* 500 in a species of *Kalanchöe*.

Diamorpha and *Sedella* are considered here to be "good" genera: their chromosome number appears to be unusual for the family, and that number is inferred to be the doubled product of the fusion between representatives of two different evolutionary streams. These genera and other Crassulaceae (a species each of *Rosularia, Cotyledon,* and *Penthorum*) with a known n-number of 9 apparently form a series of greater and greater morphologic diversity. Chromosome number and morphology seem not to be differential among *Sedella* species.

Seemingly in the Crassulaceae the trend in life-duration has been from the annual or biennial to the perennial condition. Relationships in this family are linear as well as interlinear, developmental streams having been sometimes confluent, and the taxonomic categories of the family are sharply delimited with respect to certain characters, continuous with respect to others.

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Williamsburg, Virginia,
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Literature Cited

1. Anderson, Edgar. Supra-Specific Variation in Nature and in Classification. Amer. Nat. 71: 223–235. 1937.
2. Baillon, H. Histoire des plantes. Paris. 1872.
3. Baldwin, J. T., Jr. Chromosome Numbers in Crassula. Jour. Genetics 33: 455–463. 1936.
4. ————. Kalanchöe: the Genus and Its Chromosomes. Amer. Jour. Bot. 25: 572–579. 1938.
5. Bentham, G. Plantae Hartwegianae. London. Guiliemus Pamplin. 1849.
6. Berger, A. Crassulaceae. Die natürlichen Pflanzenfamilien 18a: 352–483. 1930.
7. Böcher, Tyge W. Biological Distributional Types in the Flora of Greenland. Meddel. om Grønland 106: 1–399. 1938.
8. ————. Zur Zytologie einiger arktischen und borealen Blütenpflanzen. Sv. Bot. Tidskr. 32: 346–361. 1938.
9. Britton, N. L. and J. N. Rose. New or Noteworthy North American Crassulaceae. Bull. New York Bot. Gard. 3: 1–45. 1903.
10. ————, in Britton, N. L. and J. N. Rose. Crassulaceae. North American Flora 22: 7–74. 1905.
11. De Candolle, A. P. Prodromus, III. Paris. Treuttel et Würtz. 1828.
12. Eastwood, Alice. Studies in the Herbarium and in the Field. Proc. Calif. Acad. Sci. Ser. 3, 1: 89–146. 1898.
13. Engler, A. Saxifragaceae. Die natürlichen Pflanzenfamilien 18a: 74–226. 1930.

14. Fröderström, H. The Genus Sedum L. Pt. I. Acta Horti Gothob. 5, Append.: 1–75. 1930.
15. ————. The Genus Sedum L. Pt. III. Acta Horti Gothob. 7, Append.: 1–126. 1932.
16. ————. The Genus Sedum L. Pt. IV. Acta Horti Gothob. 10, Append.: 1–262. 1935.
17. Gray, Asa. Miscellaneous Botanical Contributions. Proc. Amer. Acad. Arts and Sciences 11: 71–104. 1876.
18. Jepson, W. L. Manual of the Flowering Plants of California. San Francisco. Independent Pressroom and Williams Printing Co. 1925.
19. Mauritzon, Johan. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Lund. 1933.
20. Michaux, Andreas. Flora Boreali-Americana, I. Parisiis et Argentorati, apud fratres Levrault. 1803.
21. Nuttall, Thomas. Genera of North American Plants, I. Philadelphia. D. Heath. 1818.
22. Pursh, Frederick. Flora Americae Septentrionalis. London. White, Cochrane, and Co. 1814.
23. Rocén, Th. Beitrag zur Embryologie der Crassulaceen. Svensk. Bot. Tidskr. 22: 368–376. 1928.
24. Rose, J. N. in Britton, N. L. and J. N. Rose. Crassulaceae. North American Flora 22: 7–74. 1905.
25. Schönland, S. Crassulaceae. Die natürlichen Pflanzenfamilien 3(2a): 23–38. 1891.
26. Sharsmith, Helen K. The Genus Sedella. Madroño 3: 1–8. 1936.
27. ————. Further Notes on the Genus Sedella. Madroño 5: 192–196. 1940.
28. Torrey, John and Asa Gray. Flora of North America. New York. Wiley and Putnam. 1840.
29. van Tieghem, P. Sur le genre Penthore, considéré comme type d'une famille nouvelle, les Penthoracées. Ann. Sci. Nat. (8 Sér. Bot.) 9: 371–376. 1899.

FURTHER NOTES ON THE GENUS SEDELLA

Helen K. Sharsmith

A New Species of Sedella

In May, 1936, shortly after publication of "The Genus *Sedella*" (Madroño 3: 240–248. 1936), a *Sedella* collected by Milo S. Baker in Lake County, California, was received for examination. Its five stamens indicated an affinity with *Sedella pentandra* of the Mount Hamilton Range, although differences were obvious. The material was too mature and too scant, however, for complete study. Mr. Baker recently re-collected this *Sedella* at the same locality, and sent fresh plants from which full diagnosis was possible. On the basis of these two collections, a fourth species is described below for the genus *Sedella*:

Sedella leiocarpa sp. nov. Herba annua erecta glabra succulenta, 3–5 cm. alta; caulis validus simplex vel ramosus, ramis e nodis inferioribus oppositis uni- vel bijugatis, quam caule primario brevioribus; cymae terminales subracemosae, simplices vel ramosae; flores conferti secundi biseriales subsessiles, 3.5–4.0 mm. longi, 3–4 mm. lati; hypanthium brevicampanulatum; petala